# Tracking Movements of Individual *Anoplophora glabripennis* (Coleoptera: Cerambycidae) Adults: Application of Harmonic Radar

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ABSTRACT Movements of 55 Anoplophora glabripennis (Motschulsky) adults were monitored on 200 willow trees, Salix babylonica L., at a site  $\approx$ 80 km southeast of Beijing, China, for 9–14 d in an individual mark–recapture study using harmonic radar. The average movement distance was  $\approx$ 14 m, with many beetles not moving at all and others moving >90 m. The rate of movement averaged almost 3 m per day. Movement patterns differed strikingly between the sexes: males averaged >6 times the total movement distance of females at  $\approx$ 2 times their rate. The overall recapture rate in this short-term experiment was 78%, but the radar tags attached to individual beetles often broke or otherwise were rendered undetectable after several days in the field. Currently, the harmonic radar system is useful for tracking beetles and obtaining estimates of their movement rates over short time periods. It will become useful for longer-term studies as more durable tags are developed.

**KEY WORDS** Anoplophora glabripennis, Asian longhorned beetle, dispersal, harmonic radar, individual mark-recapture

THE INTRODUCTION OF EXOTIC invasive species of forest insects into the United States, a seemingly inevitable consequence of burgeoning international trade, poses grave threats to our valuable forest resources (Liebhold et al. 1995, Haack et al. 1997). One such species, Anoplophora glabripennis (Motschulsky), popularly known as the Asian longhorned beetle, arrived in the New York and Chicago metropolitan areas in solid wood packing materials from China (Haack et al. 1997, Poland et al. 1998). Eradication efforts have been underway since the discovery of beetles in 1996 and 1998 in the respective areas. Potential consequences of the failure of the eradication program are dire: one recent study estimated compensatory costs for urban tree losses to A. glabripennis at >\$600 billion if the beetle becomes established throughout the United States (Nowak et al. 2001).

Dispersal is an intrinsic feature of the population dynamics of any animal species (Andrewartha and Birch 1954, Dingle and Holyoak 2001). From the human standpoint, it holds special importance for an applied ecologist trying to prevent the establishment an exotic invasive species. Eradication programs typically establish zones for intensive survey within a fixed radius of the point of entry of an introduced species, and as new infestation foci are found, new

survey zones are established in a similar manner. Knowledge of the intrinsic capacity for dispersal of an invasive species is critical for creating meaningful survey zones. In the eradication program for A. glabripennis currently in progress by the USDA-Animal and Plant Health Inspection Service (APHIS), survey areas are typically inside a 0.5-mile radius from each newly discovered infestation point (USDA-APHIS Web site at <a href="http://www.aphis.usda.gov/ppq/emergencyprograms/longhorn/survey.html">http://www.aphis.usda.gov/ppq/emergencyprograms/longhorn/survey.html</a>). Part of the rationale for this study and others (Smith et al. 2001) is to estimate the dispersal capacity of A. glabripennis so that the survey program can be as efficient, cost-effective, and reliable as possible.

Harmonic radar has been applied in recent years as a means for tracking individual movements of insects (Mascanzoni and Wallin 1986). Because the method requires attachment of an antenna or "tag," which may be heavy or interfere with flight, most applications have been to studies of movement by carabid beetles, in which flight is irrelevant for the most part (Wallin and Ekbom 1988, van der Ent 1989, Wallin 1991, Charrier et al. 1997, Lövei et al. 1997). However, the recent development of very light tags has enabled studies of movement in highly mobile fliers, such as bees, moths, butterflies, and flies (Riley et al. 1996, 1998; Roland et al. 1996; Caldwell 1997). Although characterized as a "weak flyer" (Zhou et al. 1984), A. glabripennis probably accomplishes most of its dispersal by flying (Haack et al. 1997). In this article, we present an application of harmonic radar by using lightweight tags to investigate movement in A. glabripennis. Our

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purpose is two-fold: to attempt to estimate the beetle's movement potential in aid of the current eradication program and to explore the problems and technical challenges of applying this technique to a large, aggressive flying beetle.

#### Materials and Methods

Study Site. Our study site was in Wu Qing County  $(N 39^{\circ} 23', E 117^{\circ} 00') \approx 80 \text{ km southeast of Beijing,}$ China. The study was carried out on a single straight row of 200 willow trees, Salix babylonica L., planted along the south side of a four-lane highway that ran approximately east-west through a rural area. A similar row of willow trees planted 23 m away along the north side of the highway contained most of the host trees outside the study area. Agricultural fields lay beyond the rows of willows on both sides of the highway. We did not attempt to estimate the size of the resident beetle population, but the trees hosted a moderate population of A. glabripennis adults, perhaps one or two per tree overall. Most trees had a few oviposition pits and did not manifest other signs of damage, suggesting that the site had been invaded recently.

The trees were generally spaced 4 m apart with a few wider gaps. The row of 200 study trees extended >908 m. Trees averaged 11.1 cm in diameter (diameter at breast height [dbh]) (SD = 2.06) and ranged from 5.3 to 15.5 cm. They averaged 5.1 m in height (SD = 0.93) and ranged from 2.8 to 6.6 m.

Temperatures were generally high during the study, which was carried out from 30 June through 15 July 2002; the daily maximum averaged  $33.6^{\circ}$ C (SD = 3.53) and the minimum averaged  $22.6^{\circ}$ C (SD = 2.25). Temperatures increased throughout the 16-d period, ranging from 27.8 to 40.0°C for the maxima and from 19.8 to 28.5°C for the minima. Precipitation was minimal with the exception of a heavy rainstorm that occurred during the night of 1 July. Winds were generally light. The average daily wind speed was 1.79 m/s (SD = 0.62), whereas the average daily maximum wind speed was 5.33 m/s (SD = 2.36). The wind came primarily from the south for 13 d (average direction, 200.7°, or approximately south southwest), and primarily from the north for the other 3 d (average direction, 15.0°, or approximately north northeast).

Harmonic Radar System. The harmonic detection system consists of two parts: a hand-held radio transceiver (RECCO Rescue Systems, Lidingö, Sweden) and a small "tag" that reflects the transceiver signal (917 MHz) at harmonic frequencies (i.e., 1,834 MHz) (Roland et al. 1996). When fastened to a beetle, the tag provides a unique signal against the "clutter" of the background environment (Osborne et al. 1997) that permits recapture of the beetle by using the transceiver. We should point out that the system just described is not "radar" sensu stricto. The acronym radar stands for "radio detecting and ranging." Because the RECCO system is useful for detection, but not for measuring distances, the transceiver is more properly termed a "harmonic location finder" (J. Westbrook, personal communication). However, because the



Fig. 1. A. glabripennis adult bearing a tag (d, diode; w, wire).

term is already in common use in studies of radio tracking, we will continue to refer to our system as "harmonic radar" to avoid confusion.

Tags were custom-made by hand at two laboratories: the Alberta Microelectronics Corporation (AMC) (Edmonton, Alberta, Canada) and the USDA-ARS Areawide Pest Management Research Unit (College Station, TX). A tag consists of a miniature diode with wires soldered on each side to produce a dipole antenna (Riley et al. 1996). AMC tags were manufactured from 36-gauge tinned copper wire and an unknown diode type and weighed 17.6 mg (i.e., at a length of 15 cm). ARS tags were made from 40-gauge tinned copper wire and a Toshiba ISS350 diode and weighed 11.6 mg. ARS tags were used for the first 4 d of the experiment because they were in greater supply. The two types were compared in a small test by using 10 ARS tags and 13 AMC tags during the last 2 d of beetle releases.

The tags were tested extensively before they were used in China. Tags were generally provided at 15-cm length by AMC and ARS. Ten such tags of each type were evaluated in an open field to assess their maximum detection range, and all were detected from at least 50 m. A single ARS tag was also tested for the effect of tag length on detection range by successively shortening it from 15 to 1 cm in 1-cm increments (i.e., by removing 0.5 cm of wire from each side). At 15 cm, the tag was detected at >50 m. The detection range decreased approximately linearly to 36 m at 10 cm and dropped off rapidly below that length. To ensure the greatest detection range, all tags were used at their original lengths for the experiment in China. All tags were also tested for basic functionality before they were attached to beetles.

For deployment, a tag was mounted dorsally on the prothorax and transversely to the beetle's long axis (Fig. 1). The tag was first tied to a length of dental floss, and the dental floss was then tied as a collar around the

Table 1. Movement statistics for A. glabripennis females, males, and combined sexes

Variable	Female			Male			Both		
	$\overline{n}$	Mean	SD	$\overline{n}$	Mean	SD	$\overline{n}$	Mean	SD
Total path length (m) Movement rate (m/d)	21 21	3.6* 1.9	7.9 6.9	22 22	23.5* 3.7	27.7 5.3	43 43	13.8 2.8	22.7 6.2

<sup>\*</sup> Means significantly different at the 0.05 level using a t-test.

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prothorax with the diode centered and the wires extending laterally. (NB, we tested a variety of glues initially, but no glue was found to stick adequately to the waxy cuticle of A. glabripennis so as to hold a tag.)

Release and Recapture. Seven to 12 beetles were released daily over the period 30 June to 5 July, with equal numbers of the sexes released when possible. Fifty-five beetles were released in total (27 females and 28 males). Beetles were collected from other willows planted as street trees several kilometers from the study site. Their ages were not known precisely. However, because emergence typically begins between late May and early June in Wu Qing County, the beetles were likely to have been 1–4 wk old. Beetles were identified individually with numbers in red paint on their elytra. For release, individuals were placed on tree trunks at a height of ≈1.5 m. Trees for releases each day were spaced at approximately equal intervals (usually 72 m) among the 200 trees, and no tree was used twice.

Because instruments to weigh beetles were not available in the field, beetle masses were estimated from length measurements. Lengths (i.e., from the frons to the tip of the abdomen) were measured before release. Masses of live beetles were estimated from a regression equation that related mass (M, milligrams) to body length (L, millimeters) (D.W.W., unpublished data):  $M = 0.0417 \cdot L^3 + 12.79$  (n = 12,  $R^2 = 0.98$ , P < 0.001).

Search and recapture were carried out daily from 1 July through 15 July, providing 14 d for recapture of the group released on the first date and 9 d for recapture of those on the last. The study trees were searched sequentially at a uniform rate (i.e., 55–60 s per tree) for at least 3 h by three individuals. One person scanned the canopy of a tree with the transceiver, while the others searched visually (i.e., using both binoculars and the naked eye) and identified tagged beetles as they were recaptured. Beetle identification often necessitated climbing trees and ladders. Recaptured beetles were released again after their locations were recorded.

Data Analysis. The basic estimate of movement distance was the total path length, which was simply the sum of all the straight-line displacements of a beetle from release to its last day of recapture. The constraining of beetles to move along a straight row of trees simplified the analysis. (However, it should be noted as a caveat that this constraint may also have biased the estimation of movement parameters.) Movement rate was estimated as the total path length divided by the number of days from release to last recapture. Means of these and other variables were tested for differ-

ences by sex, tag type, and movement direction by using t-tests.

#### Results

Beetle Movement. The 43 beetles that were recaptured by radar and visual means moved an average of almost 14 m, ranging from 0 to 92.3 m, at a rate of almost 3 m/d (Table 1). With almost one-half of the beetles not moving at all, the median path length was just 4 m.

Movement by the two sexes differed strikingly: males averaged >6 times the total path lengths of females and moved at twice their average rate (although the latter difference was not statistically significant). Movement patterns of the sexes were notably different as well (Fig. 2). Mostly, females did not move from the tree on which they were released (i.e., 15 of 21), and those that did move did not go far (e.g., the farthest distance was 32 m by a single female). Conversely, although some males were sedentary (four of 22), most moved considerable distances and were spread about evenly among the distance ranges up to 100 m shown in Fig. 2.

Females were appreciably larger than males. Females averaged 30.8 mm in length (SD = 2.69), whereas males averaged 27.4 mm (SD = 2.56). Estimated masses of female beetles averaged 1,262 mg (range 746–2,125 mg), and estimated masses of males averaged 894 mg (range 589–1,652 mg).

The beetles that moved did not exhibit any significant directionality in net displacement (i.e., the maximum distance east or west of the release point). Twelve beetles moved eastward averaging 22.8 m (SD = 25.4), and 10 beetles moved westward averaging 21.2 m (SD = 24.0). Once started, most beetles

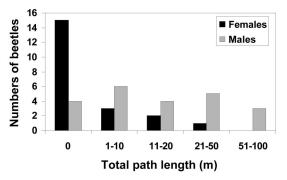


Fig. 2. Comparison of movement distances of A. glabripennis females and males.

Table 2. Recapture statistics for radar study with A. glabripennis

Variable	n	Mean	SD
Times recaptured	55	2.8	2.4
Time of final radar detection (d)	43	2.6	2.6
Time of first visual recapture (d)	26	6.2	2.6
Time of final recapture (d)	43	6.7	3.7
Proportion of total recapture period that beetles were detectable by radar	35	0.64	0.37

continued to move in the same direction, with just six individuals exhibiting minor backtracking.

Tag Performance. Considerable attrition of the 55 tags occurred over the 9-14 d that they were monitored. Nine tagged beetles were not recaptured, whereas three beetles that were not detected visually or by radar were eventually found dead. It is interesting and perhaps of significance that seven of the nine beetles that disappeared were females. Of the 43 tags that remained, by their last recapture, five entire collars (plus antennas) were missing from beetles, 10 tags had only the diode remaining (i.e., without wires), 14 tags had broken wires, and 14 tags were undamaged. Of the corresponding group of 43 beetles, 35 of those recaptured were detected at least once with the transceiver, giving a radar recapture rate of 63.6%. The remaining eight beetles were recaptured by visual means but not detected by the transceiver.

Over the 9–14 d after release, beetles were recaptured fewer than three times on average by radar or visual means (Table 2). The average time of final detection by using the transceiver was 2.6 d, whereas the average time to first visual recapture (i.e., without detection by the transceiver) was 6.2 d. These event times suggest that the tags typically remained detectable using the transceiver for 3–5 d. The time that beetles were detectable by radar was slightly less than two-thirds of the total period over which they were recaptured on average (Table 2).

The AMC and ARS tags were compared as to total path lengths by the beetles carrying them, time of their last detection with the transceiver, and time of their first detection without it (Table 3). None of the means for these variables was significantly different, although beetles bearing ARS tags traveled almost twice the distance as those with AMC tags, and the detection period for AMC tags was more than double that for ARS tags.

### Discussion

Using harmonic radar to track insects is one approach to the individual mark-recapture (IMR) method of investigating movement (Turchin 1998). IMR has some advantages over the method of mass mark-recapture (MMR) that has been used in other studies of movement by A. glabripennis (Wen et al. 1998, Smith et al. 2001). First, IMR typically has a higher recapture rate than MMR, permitting the use of relatively few individuals. We recaptured 78% of our 55 tagged beetles at least once (i.e., through both radar detection and visual sighting), in contrast with Wen et al. (1998), who recaptured 18.5% of their 1,083 marked beetles, and Smith et al. (2001), who recaptured ≈1% of 16,511. Second, IMR permits the release of marked individuals anywhere in the experimental arena, unlike MMR, in which large numbers are typically released in a single central area. Large numbers released in one place in an MMR experiment may produce artificial effects on movement through density dependence and, if recapture starts too soon and is too frequent, may skew estimates of dispersal through overtrapping individuals near the release point (Turchin 1998, Smith et al. 2001).

Conversely, IMR, at least as implemented using harmonic radar, has some disadvantages compared with MMR. One disadvantage is that IMR relies on relatively few individuals to estimate movement parameters for a large population. Because of the generally small sample size, there is a risk of missing the relatively rare individuals that may disperse great distances. Another potential disadvantage is that the marking method may hinder normal behavior. Radar tags used in this study did not seem to alter the behavior of A. glabripennis adults. They were light relative to the weight of a beetle, ranging from 1 to 2%, typically. Moreover, being mounted in front of the elytra, they did not seem to interfere with flight. On one occasion, a tagged beetle took off immediately after release and flew with great strength and direction to another tree 28 m away. Nevertheless, we cannot exclude the possibility that our tags hindered beetle flight without undertaking additional experiments.

Comparison of movement distances and rates between the current study and previous studies (Zhou et al. 1984, Wen et al. 1998, Smith et al. 2001) is problematic because of different methodologies (i.e., IMR versus MMR) and different time periods of recapture. Total path length of *A. glabripennis* adults averaged 13.8 m for our 9–14-d study, compared with a mean

Table 3. Movement and detection statistics for two types of radar tags

Variable	AMC tags			ARS tags			All tags		
	n	Mean	SD	n	Mean	SD	n	Mean	SD
Total path length (m)	13	10.1	25.1	10	19.3	24.3	23	14.2	24.6
Time of final radar detection (d)	13	4.3	3.1	10	2.1	2.0	23	3.3	2.9
Time to first visual recapture (d)	6	5.2	3.1	7	6.4	2.1	13	5.8	2.6

dispersal distance of 41.6 m over 19 d reported by Zhou et al. (1984) (for Anoplophora nobilis (Ganglbauer), which has recently been synonymized with A. glabripennis, Lingafelter and Hoebeke 2002), a mean dispersal distance of 106.3 m over 20–28 d reported by Wen et al. (1998), and a mean dispersal distance of 266 m over 9 wk reported by Smith et al. (2001). Movement rates in the current study (1.9 m/d for females and 3.7 m/d for males) were similar to the dispersal rates reported by Zhou et al. (1984) (2.2 m/d for both sexes) and slightly greater than those reported by Wen et al. (1998) (0.80 m/d for females averaged over the first 5 d after release and 0.51 m/d for males). By contrast, movement rates in our study were much slower than the dispersal rates reported by Smith et al. (2001) (23 m/d for females and 17 m/d formales). One possible reason for the higher movement rates reported in that study is that Smith and colleagues used beetles of known age soon after their emergence. Like other animal species, A. glabripennis may undergo a dispersal phase after emergence and before settling down to reproduce (Dingle and Holyoak 2001, Smith et al. 2001). Indeed, dispersal rates reported by Wen et al. (1998) declined steadily with time.

Another possible factor affecting the rate of movement was temperature. Zhou et al. (1984) reported that the optimum temperature range for adult activity was 16–28°C. Daily maximum temperatures during our study averaged 33.6°C and ranged from 27.8 to 40.0°C. These higher than optimum temperatures may have contributed to the relatively low movement rates exhibited by the beetles in our study.

A large factor in the low average movement distances and rates in our study was the high percentage of beetles, particularly females, that did not move at all. Apparently the females in our study were reproductively mature, found the release trees suitable for oviposition, and settled on them immediately to reproduce. Our study results are in contrast to others, in which females had higher dispersal rates than males (Wen et al. 1998, Smith et al. 2001). We speculate that this may have resulted from the methodology of the MMR studies. The releases of large numbers of beetles in small central locations increased their density drastically and produced a density dependent acceleration of the dispersal rate, particularly for females. Thus, the higher dispersal rates for females may be an artifact of the MMR methodology.

Nine beetles were released and never recaptured, suggesting that they may have moved outside the study area and beyond the 50-m detection range. It is interesting that seven of those beetles were females. If they indeed disappeared by flying out of the study area, they provide a behavioral contrast to those females that remained, which had relatively low movement rates. To investigate the possibility that beetles dispersed outside the study area, we made brief searches on two occasions in the row of willow trees 23 m to the north. No tagged beetles were found either with radar or visually. Some disappearances undoubtedly resulted from severe weather, in particular from

a storm with heavy rain and gusting wind that occurred during the night of 1 July. Four of the nine beetles released on 1 July were never recaptured, and three others were found dead near the study trees shortly afterward.

The development of light yet durable tags remains a challenge in using harmonic radar to track A. glabripennis. Overall, tags remained detectable for 3-5 d. Given their activities in moving through tree canopies, beetles were very rough on tags, and after a few days, the wires often were broken and twisted. This alteration of the wires from the optimal length and straight configuration lowered the detection range appreciably from the maximum of 50 m. However, this was not generally a problem, because the study trees were short, ranging from 3 to 7 m in height. Thus, the transceiver could detect tags with minor damage from underneath a tree. Eventually damage to the tags was severe enough that they were no longer detectable. Although the difference was not statistically significant, the average time of detectability of AMC tags (Table 3) was twice that of ARS tags, suggesting that the thicker wire (36- versus 40-gauge, respectively) rendered the AMC tags more durable.

Given the relatively short time that they are detectable, the tags employed in this study are useful for estimating an "instantaneous" movement rate for beetles. For example, the current system may be very useful for comparing movement rates of beetles of different ages. If tracking over a longer period is desirable, a more durable tag design is clearly needed. One possible solution to increasing durability is to develop a printed circuit on a material like Mylar (Caldwell 1997). Another might be to reinforce the tag with a thin layer of epoxy or plastic (J. Westbrook, personal communication).

In conclusion, harmonic radar shows promise as a method for tracking individual A. glabripennis adults and estimating their movement rates. Because of the fragility of the tags currently used, IMR studies are limited to instantaneous estimates of movement rate over a few days. However, longer term studies will be possible with technological improvements in the tags. Our study found many individuals, especially females, to be relatively sedentary, but a few individuals were capable of moving >90 m in little more than a week. Even small numbers of fast-moving individuals pose challenges to the survey effort for A. glabripennis in the United States that is critical to eradication of this invasive species.

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## References Cited

- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.
- Caldwell, M. 1997. The wired butterfly, pp. 40-48. Discover, February issue.
- Charrier, S., S. Petit, and F. Burel. 1997. Movements of Abax parallelopidedus (Coleoptera, Carabidae) in woody habitats of a hedgerow network landscape: a radio-tracing study. Agric. Ecosyst. Environ. 61: 133–144.
- Dingle, H., and M. Holyoak. 2001. The evolutionary ecology of movement, pp. 247–261. In C. W. Fox, D. A. Rolf, and D. J. Fairbairn [eds.], Evolutionary ecology. Concepts and case studies. Oxford University, Oxford, UK.
- Haack, R. A., K. R. Law, V. C. Mastro, H. S. Ossenbruggen, and B. J. Raimo. 1997. New York's battle with the Asian long-horned beetle. J. For. 95: 11–15.
- Liebhold, A. M., W. L. MacDonald, D. Bergdahl, and V. C. Mastro. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. Forest Science Monograph 30. Society of American Foresters, Washington, DC.
- Lingafelter, S. W., and E. R. Hoebeke. 2002. Revision of Anoplophora (Coleoptera: Cerambycidae). Entomological Society of Washington, Washington, DC.
- Lövei, G. L., I.A.N. Stringer, C. D. Devine, and M. Cartellieri. 1997. Harmonic radar—a method using inexpensive tags to study invertebrate movement on land. New Zealand J. Ecol. 21: 187–193.
- Mascanzoni, D., and H. Wallin. 1986. The harmonic radar: a new method of tracing insects in the field. Ecol. Entomol. 11: 387–390.
- Nowak, D. J., J. E. Pasek, R. A. Sequeira, D. E. Crane, and V. C. Mastro. 2001. Potential effect of Anoplophora glabripennis (Coleoptera: Cerambycidae) on urban trees in the United States. J. Econ. Entomol. 94: 116–122.
- Osborne, J. L., I. H. Williams, N. L. Carreck, G. M. Poppy, J. R. Riley, A. D. Smith, D. R. Reynolds, and A. S. Edwards. 1997. Harmonic radar: a new technique for investigating

- bumblebee and honey bee foraging flight. Acta Hort. 437: 159–163
- Poland, T. M., R. A. Haack, and T. R. Petrice. 1998. Chicago joins New York in battle with the Asian longhorned beetle. News. Mich. Entomol. Soc. 43: 15–17.
- Riley, J. R., A. D. Smith, D. R. Reynolds, A. S. Edwards, J. L. Osborne, I. H. Williams, N. L. Carreck, and G. M. Poppy. 1996. Tracking bees with harmonic radar. Nature (Lond.) 379: 29–30.
- Riley, J. R., P. Valeur, A. D. Smith, D. R. Reynolds, G. M. Poppy, and C. Löfstedt. 1998. Harmonic radar as a means of tracking the pheromone-finding and pheromone-following flight of male moths. J. Insect Behav. 11: 287–296.
- Roland, J., G. McKinnon, C. Backhouse, and P. D. Taylor. 1996. Even smaller radar tags on insects. Nature (Lond.) 381: 120.
- Smith, M. T., J. Bancroft, G. Li, R. Gao, and S. Teale. 2001. Dispersal of Anoplophora glabripennis (Cerambycidae). Environ. Entomol. 30: 1036–1040.
- Turchin, P. 1998. Quantitative analysis of movement. Sinauer, Sunderland, MA.
- van der Ent, L. J. 1989. Individual walking-behaviour of the carabid *Carabus problematicus* Herbst in a Dutch forest has been recorded by a radar-detection-system. Netherlands J. Zool. 38: 104.
- Wallin, H. 1991. Movement patterns and foraging tactics of a caterpillar hunter inhabiting alfalfa fields. Funct. Ecol. 5: 740-749.
- Wallin, H., and B. S. Ekbom. 1988. Movements of carabid beetles inhabiting cereal fields: a field tracing study. Oecologia (Berl.) 77: 39-43.
- Wen, J., Y. Li, N. Xia, and Y. Luo. 1998. Dispersal pattern of adult Anoplophora glabripennis on poplars. Acta Ecol. Sinica 18: 269–277 (original in Chinese).
- Zhou, J., K. Zhang, and Y. Lu. 1984. Study on adult activity and behavioral mechanism of Anoplophora nobilis Ganglbauer. Scientia Silvae Sinica 20: 372–379 (original in Chinese).

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